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VISUAL ACUITY AND ITS DEPENDENCE UPON RECEPTOR DENSITY AND RETI--ETC(U)
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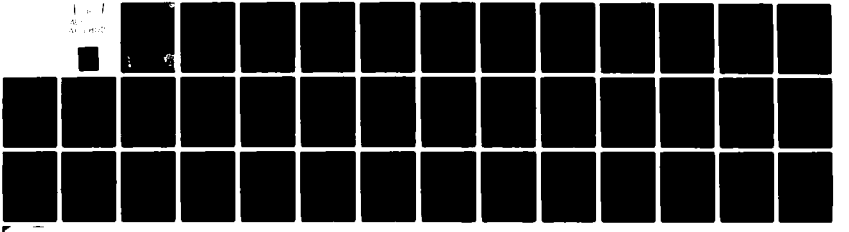

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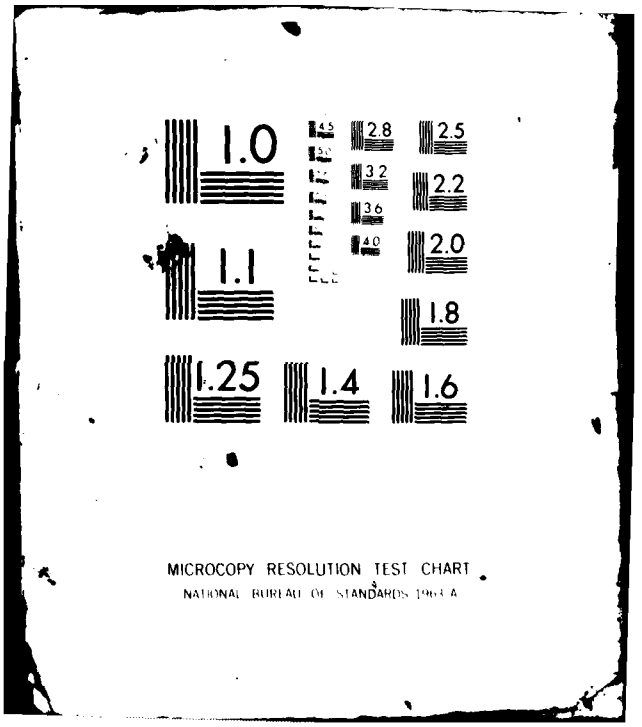
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FINAL REPORT

NAVAL AIR SYSTEMS COMMAND CONTRACT N0019-80-C-0393

Visual Acuity and its Dependence Upon Receptor Density and Retinal Ganglion Cell Receptive Field Overlap

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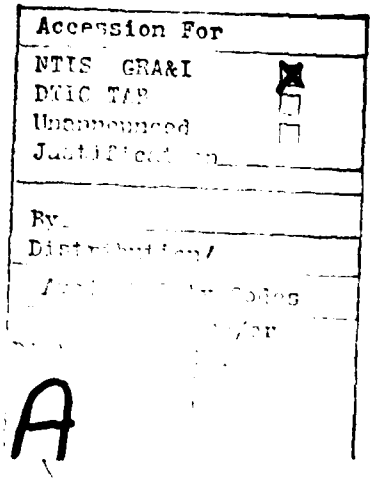

ABSTRACT

The organization of the retina has been investigated with regard to visual acuity. In particular, the receptive fields of the ganglion cells have been analyzed and described in terms of, primarily, their anatomical relations to each other, i.e., receptor spacing and secondly, the neural organization. In a typical eye (cat) the sensitivity to angular separation on the basis of anatomical makeup has an upper limit of 8 cycles per degree for acuity. On the other hand, it is predicted that, for neural processing of overlapping ganglion cell receptive fields in the retina, that the behavioral response should be at least twice as good, i.e., approximately 16 cycles per degree. The different methods of analyzing receptive fields compare the sensitivity of the receptors with a static stimulus (sensitivity profile and Ricco field - area x intensity - test), and displacement sensitivity (the response to a small stimulus spot switched between the two positions just touching each other). Present data, which indicates that in the area of high sensitivity in the cat retina at least 15 receptive field centers must overlap, leads to the conclusion that the retinal visual acuity is not limited by the receptive field size, but rather displacement sensitivity and the processing of the information by higher visual centers.

INTRODUCTION

This program has been designed to examine the cellular basis of spatial vision and, in particular, to describe and analyze the factors limiting spatial vision with regard to fine detail or acuity. The theoretical basis behind an analysis of spatial vision is not as well defined as for color vision. In the field of color vision, recording the coded messages from single neurons came after extensive theoretical models on the basis of psychophysical data had been established. Even though this model was considerably modified by the information gained from the electrical physiological data, nevertheless, the main problems, with hints of possible solutions, were already apparent. However, for spatial vision, much of the theoretical work has been done in parallel with the experimental work. Most theories of visual acuity have postulated that the limit to the ultimate visual acuity that can be obtained either theoretically or practically is set by the relation

of the photoreceptor sites in the retinal mosaic with the retinal image size. It requires a point-to-point presentation at each receptor in the cortex. This theory was originally postulated by Helmholtz (1852) and has been considerably modified in recent years by Stone (1965), Green (1970), Harter (1970), and Snyder (1975). The portions of the image on the retina that are near the limit of visual acuity are small enough so that the wave properties of light itself determine the intensity of distribution. Something so distant in visual space that it is a point source for geometrical optics (a star, for example) is focused on the retina, not as a point, but, rather, as a diffraction limited image (point-spread function). This particular type of imaging has been treated in previous reports in connection with visual acuity (Wolbarsht and Ringo, 1978, 1979, 1980). The details of the diffraction limited image are then dissected by the receptors.

One important optical aspect of the retinal mosaic is the minimum center-to-center spacing of the receptors. Those sizes, shapes, and relative refractive indices of the receptors, all of which determine any wave guide-like action, are equally as important (Snyder 1975). A majority of the analyses of visual acuity in relation to the retinal mosaic have been concerned with how the retinal anatomy is matched to the image on the retina as calculated and measured with the point-spread function.

All models based on such analyses contain the implicit assumption that information through the visual system represents a point-to-point-topographical representation of the retinal receptor mosaic up to the cortical level. Thus, as an end result, each retinal receptor is represented in the cortex by a single cell or a group of cells. In these models, the responses of a cortical cell contain coded messages representing the intensity of light on the appropriate retinal receptor. In the simplest model, the pulse frequency arriving at the cortical neuron is a simple and unambiguous function of the intensity of light falling on the retinal receptor. In this model, decoding the message consists of relating the pulse frequency to the stimulus intensity, and recognizing the position on the retina which corresponds to that cell. Adjustments for the spectral sensitivity of the cell allows the visual image to be put together with the intensity changes and color presentation at the right portion of visual space. However, the details now available of the anatomical structures in the visual system, and the electro-physiological function of all cells which are presently known are not compatible in any way with the strict point-to-point representation for information transfer from single retinal neurons to the single cortical cells.

In the retinas of non-primate vertebrates, and in the extra foveal region of primate retinas, each ganglion cell must be connected to large numbers of receptors, as the receptors far outnumber the ganglion cells. In the primate foveal region where the visual acuity is the

highest, the histological analysis of the retina suggests that there is a nearly one-to-one relationship between receptors and ganglion cells, with, however, slightly fewer ganglion cells than receptor cells (Missoten, 1974). In any model of the visual system which has a point-to-point representation, there must be as many ganglion cells as receptors and the connections between them must be simple. Evidence that a high degree of visual acuity can be obtained without this particular organization can be found in some animal eyes. For example, in hawk and eagle eyes, the optics and visual acuity are as good as, if not better than, in humans (Schlaer 1972, Miller 1976, Fox et al. 1976). However, in the hawk and eagle foveas, the receptor to ganglion cell ratios is quite different from that in the human fovea. In both of these birds, there are at least three, and possibly ten, receptor cells per gangion cell (Miller 1976, Fite and Rosenfield-Wessels 1972). This indicates that high visual acuity does not require as many ganglion cells as receptors. Furthermore, in these visual systems, at least, point-to-point representation of the receptor stage throughout the visual pathway cannot be compatible with the type of anatomy actually found. For example, in the geniculate and optic tectum, there are many examples of convergence and divergence of the connections from a single cell in its ascending projections.

Another point is that in the human retina, acuity does not change abruptly along any isoptors toward the periphery from the fovea. Although the best visual acuity is in the central portion of the fovea

(perhaps 20/15 or 20/10) as progressively more peripheral portions of the retina are sampled, the acuity declines to 20/30 and so on outside the fovea. The function of change is a smooth one, yet extra foveal regions cannot possibly have a one-to-one relationship between ganglion cells and receptors, there being far fewer ganglion cells. This is a very quick shift in all members, the lack of such a junction in this function, in itself, argues against any simple one-to-one projection. It is extremely unlikely that one portion of the retina has its own specialized type of information processing and that those bordering upon it abruptly shift into a completely different system without any disjunction. Also, there is not a sense of a change from one type of neural processing to another under real operating conditions.

There is an additional consideration which is usually ignored in computing the ratio of receptors to ganglion cells: ganglion cells are not all the same. They are not at all equivalent to each other in their function. On the basis of these differences in function, they can be grouped into several distinct categories. As some categories may not be involved with visual acuity, the ratio of these ganglion cells which are responsible for acuity in vision to the receptor cells may be far less than has been calculated from simple anatomical examinations which count all ganglion cells as equivalent. Ganglion cells carry many different types of information in a sort of time-sharing relationship. They carry the intensity information required for border contrast, possibly the basis for acuity, along with

information about color contrast. It is important to recognize here that information can only leave the retina through these ganglion cells. Thus, they act as the final common pathway for all neural messages to higher visual centers.

Within the visual system, there are neural mechanisms which act to increase contrast by amplifying small differences in intensity (Ratliff 1965, and Georgeson and Sullivan 1975). This was, of course, originally an effect described in psychophysical terms by Ernest Mach. The physiological basis of this effort was, in elegant detail, discovered in the visual system of the horseshoe crab by Hartline et al., (1954). Obviously, this process could aid special resolution by enhancing the contrast of borders and image. However, such a type of information processing has not been seen in a clear cut fashion in any vertebrate retinas. But a ganglion cell, at least, must form the basis for parallel interaction to achieve such a type of contrast. Although contrast phenomena are easily seen in the primate retina with regards to color, the manipulation of parameters associated with pattern vision have not yet shown such a clear cut effect. It is possible that some distortion of the information by the receptor to ganglion cell connection, may form the fundamental and ultimate limit to visual acuity. This will be shown later in this report. It is possible that motions of the image within the receptive field of the ganglion cell at or near the junction between the input processes (cones) which

contribute to the center and thus, contribute to the surround portion, may define the ultimate limit of visual acuity.

In this program, the neural organization of the retina for visual acuity was investigated to determine how it contributes to the appreciation of low visibility targets. Data collected on the size and organization of retinal receptive fields in monkeys and cats has been used to model the information flow to the retina in relation to the psychophysical measurements of visual acuity, and the anatomical cytoarchitecture of the retina. Modifications of the retina, which act to increase visual acuity, has been plotted by electrophysiological techniques. The experimental measurements of receptive ganglion cells made in the area centralis of cats furnish the most useful data for the construction of the model. In this region the receptive field sizes of X type ganglion cells were found to be much larger than required simply to cover the total area. The center diameters covered a visual angle of about 0.4 degrees. This provided an overlap of about 15 adjacent receptive field centers for any one point in visual space.

The ganglion cell receptive field spatial sensitivity exhibited serious discrepancies between two methods used to gather data, and Ricco field plot in which the relationship of area vs. intensity was measured, and the profile of the receptive field sensitivity as plotted with a small exploratory stimulus spot. The resolution of this discrepancy indicates that the ganglion cell receptive field

sensitivity found in any given situation is partially a function of the duration of the visual stimulus. The ganglion cell sensitivity profile also revealed anomalous behavior when measured by the sensitivity to saccade-like movements of a small stimulus spot. The highest sensitivity to movement occurs at the center-surround border rather than in the center of the receptive field where the normal on-and-off responses have their highest sensitivity.

These experiments clearly indicate that visual acuity must have, as a functional basis, the comparison of signals from adjacent and overlapping ganglion cell receptive fields. This overlap allows not only that the desired features in visual space are precisely located, but also confers an overall low sensitivity to noise in the visual system. In the cat, it appears that at least 15 ganglion cells are involved in a localization of any given point in the area of highest visual acuity. This data should be applicable in primates and man in the fovea, the region of highest visual acuity, as a similar organization for information analysis is presumed to operate there, in the highest visual centers, at least.

EXPERIMENTAL PROCEDURE

Types of Animals Used

Three types of monkeys were used in the present study, rhesus (Macaca mulatta), the Himalayan Macaque (Macaca assamensis), and the crab-eating or cynamolgus (Macaca fascicularis). All were essentially identical in terms of the recordings from the eye. However, the bone structure of the head differed among them, especially in the older animals. The younger animals had less prominent brow structures which made recording from the central portion of the eye much easier. They all survived the anesthesia quite well in repeated experiments. Most remained healthy during the course of the program, although one died of Shigella infection. Attempts were made to trade the animals with local users in order to obtain favorable facial structure for electrode placement.

Anesthesia and Surgery

All experiments were carried out under general inhalation anesthesia as described in previous reports (Wobarsht and Ringo 1979, 1980, 1981). The animals were initially anesthetized with ether. When a suitable depth of anesthesia was obtained, an intravenous infusion of gallamine triethiodide (Flaxedil) 5 to 10 mg/cc in saline was initiated at the rate of 20 to 30 mg/kg of body weight/hr. The animal was then

intubated and respired artificially with a ventilator (Harvard Apparatus Company Model 661). Anesthesia was maintained with 70% nitrous oxide/30% oxygen mixture in all animals throughout the experiment. Expired pCO_2 was monitored continuously by a Beckman Model LB-1 medical gas analyzer with the aid of an indicator alarm (Electrodyne MS-25). The CO_2 level was kept at 4.7%. In addition to the control of gas mixture flow furnished by the anesthesia machine (Ohio Chemical and Surgical Instrument Company, Model 212B), a manometer was installed to avoid any damage to the animal's lungs from overpressure during the inspiration and exhalation parts of the respiratory cycle.

The infusion of Flaxedil with dextrose and saline was continued throughout the experiment to assist in fixing the eyes. A local anesthetic (5% lidocaine ointment) was applied to the surface of the conjunctiva before an incision was made to insert the electrode into the eye, and to all other incision margins and pressure points. Animals were maintained at normal body temperature by means of a heating pad. These life support systems were adequate to maintain a cat in satisfactory physiological condition for 24 to 48 hours.

Although nitrous oxide, even at high pressure, does not produce surgical anesthesia (Brown, et al, 1927, Venes et al, 1971), it has been established that 70% nitrous oxide in oxygen produces a high degree of sedation and analgesia in the cat and monkey and is an

adequate anesthetic where only mildly noxious stimulants are present; for example, the direct electrical stimulation of peripheral nerves at frequencies up to 3 Hz, or foot pad shock (Venes et al, 1971). In our experiments, the animals are under deep ether anesthesia during all surgical procedures. The level of ether anesthesia was sufficient to terminate spontaneous respiration and the animal required artificial local anesthetic. Only after surgery was ended was the ether discontinued and 70% nitrous oxide/30% oxygen used. The insertion of the electrode through the pars plana involved no pain and is similar to operations that are often carried on in humans with only a local anesthetic. The heart rate was continuously monitored and at no time were heart rate changes detected which could be associated with pain perception.

The gallamine triethiodide (Flaxedil) drip is not required to relax the animal. It assists in establishing the high degree of eye immobility required for single cell retinal recordings (Enroth-Cugel and Robson, 1966). It has also been established that Flaxedil has no effect on retinal ganglion cell responses (Enroth-Cugel and Pinto, 1970). Because of these considerations, nitrous oxide and Flaxedil have been routinely used by many workers in this field.

Nitrous oxide is used by us and others because it has been shown to have only slight effects on evoked CNS responses as compared to the strong central depression produced by other volatile anesthetics and

barbiturates (Van Noren and Padmos, 1977). A depressive action in the retina has been seen with some of these anesthetics as well (Van Noren and Padmos, 1977). It is, obviously, important to minimize drug effects on the CNS when studying the activity of the visual system.

The iris was dilated and accommodation relaxed with several doses of Duke mix (10% phenylephrine; 0.5% Mydriacyl, 1:1) applied every hour.

Optical Stimulus

The optical stimulator has been described previously (Wolbarsht, 1978) and has two channels with essentially equivalent pathways. Each channel could be varied independently and includes a collimated region to allow the use of interference filters. The characteristics of the interference filters have been given in a previous report (Wolbarsht and Ringo, 1979).

A Maxwellian view was used for the stimulus, and the field aperture of the optical stimulator was focused on the retina forming an approximate 0.02 mm spot. The spot size was estimated by comparison with known apertures in focus on the retina, a demagnification factor related to the size of the disc, and the known size of probes inserted into the eye. The stimulus beam was approximately normal to the retina to eliminate any changes in the stimulus-response relations from

the Stiles-Crawford effect. A third channel is available, which is suitable for chromatic adaptation of the entire retina through a series of Wratten filters described previously (Wolbarsht and Ringo, 1979).

The optical system output was calibrated with an Epply thermopile (Type 12 junction linear with a quartz window). The sensitivity of this thermopile, in turn, was calibrated against a secondary standard lamp, Epply Type NALCO A-10, whose initial calibration is traceable to the National Bureau of Standards.

The electrophysiological recording equipment is as described previously (Wolbarsht and Ringo, 1979).

Experimental Design

Most data points were measured with a constant response technique. That is, when any selected parameter of the stimulus was changed, the intensity was varied sufficiently to obtain a response equal to the criterion one under the original test conditions. Some data points were obtained by a silent substitution technique. In this technique, the stimulus was alternated from one wavelength to another, or from one spatial location to another, while the intensity of the stimulus with the altered parameters was changed to minimize or eliminate the response. Although this technique has problems, as some ON responses may be confused with OFF responses, a selection of the proper type of

chromatic adaptation usually allows a balance to be reached, and, in this way, quite accurate data can be obtained. Spatial isolation (center or surrround presentation only) of the stimulus can also be used to assist in elucidating the spectral sensitivity within a ganglion cell receptive field, which is composed of the various cone systems in addition to the rod contribution.

RESULTS AND DISCUSSION

Receptive Field Sensitivity Profile.

As discussed in previous reports, there are two methods for examining receptive field sensitivity. Both are widely used. The small exploratory spot method and Ricco field plot method (Rodieck, 1973, Wagner and Wolbarsht, 1958). As the name implies, the small exploratory spot method uses a small spot of light to sample the sensitivity of the ganglion cell's receptive field. As the peripheral portion of the receptive field is approached, the intensity of the stimulus spot must be very large, and scattered light also makes an appreciable contribution to the response. The Ricco plot method measures the threshold intensity for a series of varying diameter circular stimulus areas concentric with the ganglion cell receptive field. The series usually begins with the smallest diameter available and goes to the largest possible with the optical stimulator. The intensity which must reach the minimum detectable threshold is plotted against the stimulus size for a series of the entire range.

One problem with the use of the two methods of plotting the field in the past has been that the results do not correlate well with each other. There are two areas of disagreement:

1. The fall-off of sensitivity in the more peripheral regions of the receptive field is different with a small test spot than is found with the Ricco method. That is, the fall-off in sensitivity tested with a small spot seems, to a very large extent, to have no appreciable break in it. For a comparable wavelength and duration stimulus, the Ricco plot will have a finite size with no appreciable contribution or even an inhibition from more peripheral regions.

2. Sensitivity profiles do not match with the Ricco field plots The resolution of this problem may be primarily a lack of identity of the two experimental situations, and secondly, a possible built-in artifact in this method of obtaining Ricco field data.

In the first case, a small spot stimulus response does not really conform to the assumptions of the constant response criteria. The responses seen are constant, but since we are recording from a third order neuron ganglion cell, we are using progressively more and more peripheral receptors and they must be stimulated at higher and higher rates. This assumes a linear fall-off of response as a function of intensity that is not completely justified. Also, the intermediate neurons are more or less stimulated than the higher order cells, but their responses affect the selected ganglion cells to a lesser degree. Thus, again, we assume a linear response relation in them for a much wider range in the periphery than in the center. If the response is not completely linear, then the shape of the profile will be distorted

in increasing amounts. However, with the Ricco plot, the linearity of the system is tested as far as spatial integration goes. However, since the stimulus has a finite duration and the ON responses must be separated from the OFF responses, generally a stimulus of rather long duration is used. Usually this is much longer than the integration time of the ganglion cell.

Experiments in the goldfish and carp eyes illustrate this point. The fish retina has an extremely long integration time, and thus, a longer duration of stimuli can be used to give better time resolution of the effect. H.G. Wagner has suggested that the different shapes of the sensitivity profiles of the red and green cone inputs to the ganglion cell may be due to an experimental artifact, the variation of the effective stimulus time.

The integration time of the ganglion cell is that period of time during which there will be more or less complete integration of all light absorbed by the receptors connected to it in more or less equal fashion. After this integration time (usually about 0.01 sec), the ganglion cell is less and less affected by the stimulus. However, the Ricco field plot, since more and more peripheral portions of the receptive field are progressively stimulated, has a problem in that a finite time is required for transmission of the neural signal from the peripheral portion of the receptive field to the ganglion cell. This means that during a long stimulus a certain distance is reached, the

neural signal will reach the ganglion cell after the integration time. However, if the stimulus is given very rapidly, then the size of the area of the receptive field in which the Ricco field plot time-intensity relation is constant, can be extended. As the area increases, the threshold will decrease as more and more receptors are stimulated.

The Ricco Plot varies in its extent of integration in the area as a function of the length of the duration of the stimulus. The longer the stimulus duration, the smaller the cutoff area for integration. This indicates that the summation time for the response of the ganglion cell may be the most important factor in determining the size of the receptive field as seen experimentally. A very short pulse will allow the peripheral regions to get their full stimulation early, and may allow them to pass their input on to the ganglion cell before its cutoff time for the threshold response.

The changes in the shape of the receptive field profile in the central plateau size have been matched with the duration of the stimulus pulse. When a long pulse (0.5 sec) is used, only a short part of it will be effective as a stimulus for the periphery. Short pulse times must be used in order to make certain that the peripheral regions could activate the ganglion cell within its summation period.

However, the discrepancies between these two types of plots do not influence the central thesis in any real retina. Mainly, in any way that receptive fields are plotted, the receptive fields will be large and there will be considerable overlap between them. Thus, any discussion on visual acuity must take account of this overlap and consider its contributions for good or bad.

The overlap of receptive fields has been discussed in detail previously (summarized in a report by Wolbarsht and Ringo, 1980). The main advantage is the noise reduction in the system. That is, noise in the receptor signal is reduced by comparisons between the signals from the overlapping fields. When the 13 receptor field model is compared with the 3 receptor field, and the reduction is in noise, approximately the difference between the number of receptors in the two fields. Since ganglion cell receptive fields in the cat have at least 20 cone inputs, a correspondingly larger reduction in noise would be possible. This would aid with visual acuity and border location, although, possibly it would not work for color mechanisms. Another advantage of the overlapping receptive fields is, of course, the reduction in the number of ganglion cells required for localization. However, this is not achieved without some sacrifice. There is a trade-off between the number of ganglion cells and the number of, or amount of, fine detail in the visual space that can be appreciated. Although the acuity may be as high with a few ganglion cells, only a few points can be discriminated at any one time. Thus, with a very rich visual

environment, there may be confusion within the neural processing system, if the number of ganglion cells is restricted.

The interaction of visual acuity with chromatic information restricting the spectral bands can eliminate some optical aberrations where both chromatic and spherical forms exist. Nevertheless, this cannot be carried too far, as indeed, it is necessary to have color discrimination at least, since color perception is present in the photopic range and, thus, it must interact with visual acuity. The optical contributions to visual acuity can be discussed in later sections, especially as regards the sectional specializations of the retina in regard to receptors and receptive field organization.

Static and Displacement Sensitivity in Ganglion Cell Receptive Fields

The coding of object (image) motion, even with a preferred direction, has been studied extensively in the neural information of the retinal ganglion cell. This effect has been found, particularly in the frog, but also in some mammals (rabbits) and in birds. In monkeys and cats, a higher order of response neurons in the lateral geniculate and the cortex, made up of various combinations of inputs from neurons in the preceding stages, have also been found. However, in the cat and monkey, and presumably also in man, there are no clear cut examples of motion detection at the retinal level. It is difficult to construct a model, using ganglion cells as motion detectors, that simultaneously

gives information on visual acuity. The motion detection cells were elaborately discussed by Lettvin and co-workers on their classic examples in the frog retina.

However, the type of information present in retinal ganglion cells in the cat seem to, in some degree, use that small extent motion of the image to give acuity information rather than be a form of motion detection. A typical cell is shown in Figure 1. The first profile gives the sensitivity for the appearance or disappearance of a small test stimulus. The highest sensitivity is in the center of the receptive field, which is relatively a very small area with a smooth fall off on either side. When the same test stimulus is, however, moved slightly, then a response again is given. In this case, however, the highest sensitivity for motion is at the junction between the so-called surround and central fields. The antagonism between excitory and inhibitory phases seems evenly balanced at approximately 0.15 mm, as the receptive field is more or less symmetrical in this respect. Most other cells give this kind of information and probably this type of response is most closely related to that assumed in physiological situations.

In the physiological situation, the type of information used for visual acuity, and most other visual information, is not occasioned by the abrupt appearance of a test object as an important feature of the visual environment. Extreme contrasts of light on dark, or dark on

light are not present, nor does the object have an abrupt appearance in the same manner. Rather, there is appearance of objects of moderate contrast with respect to the background, which then moves to some extent. Even if the object itself does not move, the normal physiological tremor and other small eye movements do produce a motion, to some extent, of the image on the retinal mosaic. This will be effectively detected by this certain portion of the receptive field, the border between the center and periphery. A large movement in this case, of course, will be the same, of abrupt appearance and disappearance, for an individual ganglion cell to give the static type of response. In the present case, however, the movements are so small that an entirely different type of response is activated. This is one that may be, finally, one of the most important for visual acuity under physiological conditions.

It is true that high visual acuity can be achieved with very brief flash presentations. However, in this case, the mechanisms may be more akin to the static type of detection by the central ganglion cells rather than the more eccentrically located detection of the micro-motion in the detail of an object.

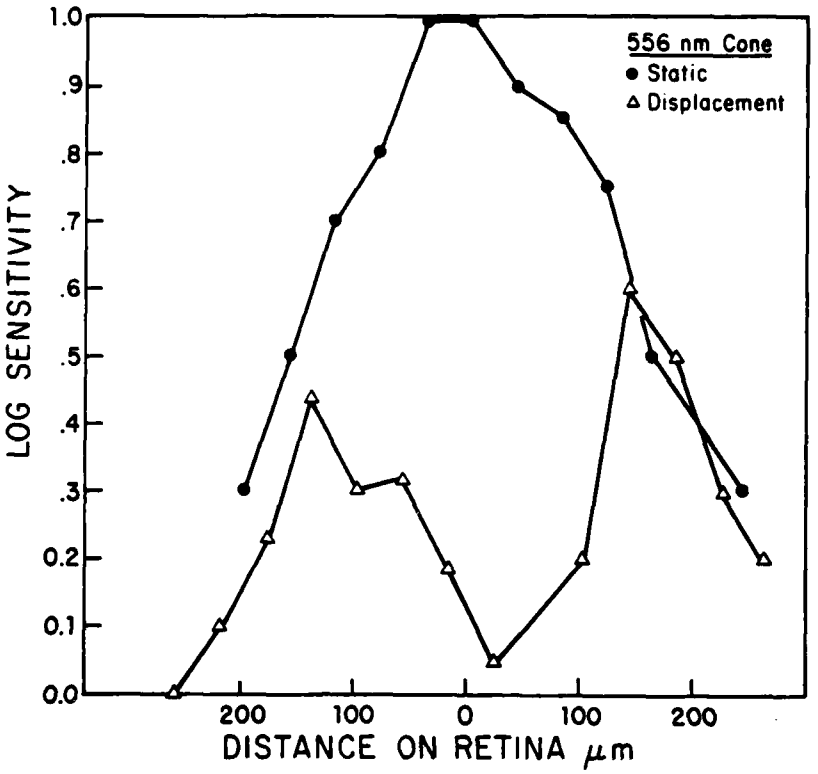

FIGURE LEGEND

Figure 1. The Receptive Field Profile for an On-Off and Displacement Sensitivity of a Retinal Ganglion Cell in the Cat

The filled circles give the threshold responses to a 0.035 mm (10 minutes of arc) circular yellow (580 nm) stationary stimulus spot, alternating light and dark at 0.5 Hz. A blue background adapting light used a Wratten #47 filter for adaptation of the rods equivalent to 6.0 times 10^{-10} photons/deg^{-2} sec of 500 nm light. This blue background assured that the responses were from the 556 nm cone input.

Displacement sensitivity (open circles) was measured with a 0.035 mm (on the retina) spot which was jerked suddenly (in less than 0.1 sec.) between two positions. This corresponds to a 10' of arc displacement in the visual field .035 mm apart. Between each displacement the cell remained unstimulated for one second. The displacement sensitivity points are plotted intermediately between the two rest positions. Zero log units on the sensitivity axis is 1.75 x 10^{-11} photon/deg^{2} sec. at the cornea. Negative log sensitivity numbers are for the OFF responses from the surround input process, and should be read in their absolute values only.

Anatomical Variation in the Retina and Their Contribution to Visual Acuity

An analysis of the data in this study, together with other published material, all suggest that the receptive field of each ganglion cell contains the same number of cones. However, as the size of the receptive fields increases and the border between the center and the surround grows as the receptive field is located more and more peripherally in the retina, i.e., further toward the equator and away from the area centralis, it seems that the visual acuity should change with regard to the size of the receptive field. Other factors are also operative, and their contribution must be assessed separately. For example, the image changes with the position in the retina in many ways. The central retina is compared with the peripheral portions in the following discussion to illustrate the differences.

The retina is organized in man and other primates so that light reception by the photoreceptors--cones and rods--is followed by the processing of this information in the other retinal neurons. The ganglion cell is the final summing point in the retina. The optic nerve fibers of ganglion cells transmit the summed information from the whole retina back to the lateral geniculate and other higher visual centers. However, it is in the retina that the primary detection of visual detail occurs. Initially, the photoreceptors begin the process, but the actual site of the initial analysis of detail may be in the

synaptic connections to bipolars or other retinal neurons. However, the ganglion cell receptive fields topologically differ in the various parts of the retina. These differences, to some extent, depend upon the optics of the eye. An analysis of the physiological optics of the human shows that receptive field size may be partially a modification of a simple function of retinal position. The following section discusses this relation.

The Relation Between The Optics Of The Eye And The Organization Of The Retina For Information Processing With Reference To Visual Space

The optical system of the eye has many problems, some are common to all optical instrumentation; others are peculiar to the eye-brain combination, such as the differential light and color adaptation which accentuates all problems. The sizes of the ganglion cell receptive field in different parts of the retina also seem to be related to optical properties of the eye, particularly those related to the wide field of vision. The eye can see almost 180 degress, and external boundaries, such as the nose, rather than the optical characteristics of the eye, impose the real limits on the field of vision. The eye must, then, have many special characteristics to have such an extremely wide field of vision. The most important of these is vignetting, the fall-off of the intensity on the periphery of an image. The name itself comes from photographic vignetting techniques of putting a fuzzy

border around a portrait. At the larger angles of divergence from the optical axis of a lens system, as in a wide angle camera lens, the dimming is very noticeable, However, there are several kinds of optical effects covered by the term vignetting which can be easily shown with a simple lens system example. The major effects come from variations in the object image-distance and pupil obliquity.

Object-Image Distance

In a simple optical system with a plus lens, the peripheral portions of the object and its image are further from the lens than the central portions. With the inverse square law, the intensity of the image varies with the $\cos^4$ of the angle of divergence. That is, the periphery of an extended object is lower in intensity at the lens than the central portion, and the intensity of the object varies in the same way. In photographic terms, the f number of the system increases towards the peripheral portion of the image. In the vertebrate eye, and in particular, the human eye, this particular form of vignetting is eliminated because the image plane, the retina, is not flat but curved, The retina is the surface of a sphere, but the nodal point of the eye's optical system is not the center of that sphere.

The eye has a complex optical system with two nodal points, but a simplified equivalent of the eye with a single nodal point is sufficiently accurate for the following discussion. The peripheral

portions of the retina are closer to the nodal point than the central portion. The spherical aberration of the eye's optical system, however, keeps all portions of the image in focus on the retina. Indeed, the change in focal distance largely compensates for the spherical aberrations of the cornea. Since the distance from the nodal point to the peripheral retina is less than to the central portion, its image is smaller than in the central portion of the retina. That is, the photographic f number of the system is lower in the periphery than in the center, almost exactly compensating for the change in the in the distance of the object from the cornea. This makes the image in the periphery smaller, but just as bright as in the center.

Pupillary Obliquity

The pupil is reduced in area as the view of it becomes more oblique. This is a function of the object position and its deviation from the optical axis. This also causes vignetting. In order to understand this particular optical problem, it is necessary to examine both the effective area of the pupil, and the structure of the retina in detail. Most of the vignetting effects are compensated for by the shape of the eye, the curved image plane of the retina, as discussed above. However, as the area of the pupil decreases for more and more peripheral objects. This produces a real change in the intensity of the retinal image as shown in Table 1. Interestingly enough, this change in intensity is not perceived. The structural characteristics of the retina

may compensate for part of this anamoly. The changes in the receptive fields of ganglion cells may account for the rest.

The retina changes in structure markedly from its peripheral portions to its optical center, the fovea. For example, the photoreceptors, especially the cones, have shapes in the periphery much different from the central ones (see Snyder and Miller, 1968 for review). The central cones have long, thin cylindrical inner and outer segments. Indeed, in shape they can hardly be distinguished from rods. On the other hand, the cones in the peripheral portion of the retina have very short, fat outer segments which taper to a point, thus, giving the name "cone' to this group of cells. The differences in diameter between the central and peripheral cones are also quite marked. The peripheral cones have a diameter more than twice that of the central ones.

The difference in shape between central and peripheral cones is most marked, by far, when area is examined. In the center, a cone occupies approximately the same area on the retina as a rod, almost a one-to-one relationship. The peripheral relation is quite different, the area of one cone is equivalent to about 20 rods. Partially, this change is connected with the wave guide nature of the peripheral cone outer segments to send all photons not at wavelengths well absorbed by the cones into the rods for use in scotopic vision (Snyder & Miller, 1968). In the human eye, those rejected wavelengths are well absorbed

by the rods, and act functionally as a tapetum, thus, making for a very energy efficient system.

Another effect connected with the change in the shape of the cones is that found by Stiles and Crawford (1938). Light entering the peripheral portion of the pupil is less effective for stimulating the cones than the light entering through the central portion of the pupil. This effect is especially marked at the pupil sizes, and the larger eccentricities of the image from the optical axis. However, the Stiles-Crawford effect is not noticeable when the pupils are somewhat constricted under photopic conditions. At light levels at which the cones are physiologically active, the pupil size is usually 3 mm or less. Thus, in a laboratory situation, where a large pupil can be produced, the Stiles-Crawford effect can be demonstrated easily. In the normal physiological situation, it does not seem to be operative, and can, thus, be ignored in an analysis of the visual components of an operational situation.

Table I

RELATIVE ENTRANCE PUPIL AREA FOR VARIOUS DIAMETERS AND ECCENTRICITIES IN THE HORIZONTAL MEDIAN

Object Eccentricity deg°	Actual Pupil Diameter mm			
	8	6	4	2
	Relative Apparent Area of Pupil			
0	1	1	1	1
25	0.94	0.94	0.94	0.94
50	0.76	0.76	0.76	0.76
75	0.44	0.44	0.44	0.44
85	0.25	0.27	0.29	0.30
95	0.094	0.114	0.132	0.15
100	0.030	0.042	0.053	0.064

Possibly, the changes in cone size in the periphery may be sufficient to compensate for this change in retinal illumination when moving from the center to the periphery (Snyder and Miller, 1968).

The effective area of a cone in the periphery increases just enough to compensate for the lower intensity due to the decrease in pupil area with increasing eccentricity. The increase in the area of the cone has a very close, good reciprocal relationhip with the decrease in the area of the pupil at the same angle. Thus, even though the photon fluxes is quite different, the same number of photons impinge on the cones in the periphery as in the center.

The peripheral cones have just as much visual pigment as the ones in the center. This amount seems to be necessary for the proper function of the cones.

The perception of even illumination from all parts of the visual field under photopic conditions is dependent upon having the same neural signal from the cone receptors. Unless some neural mechanism is inserted to weight the original photo reception, there will be a decrease in response as a function of position in the retina. Neural weighting is, of course, not impossible, but the number of photons entering the eye is small and a noise problem will very quickly arise with the peripheral signals. Some structural adaptations must be made which adjust the receptor photon flux to be comparable with that in the center. Again, if it is assumed that the photon

flux has been adjusted so that the neural signal from all photoreceptors is approximately the same to get the same signal out of the cones, then this requires that approximately the same number will be connected to the ganglion cell. This, in turn, because of the change in the distribution of the photoreceptors (rod and cones) in the different parts of the retina, leads directly to a change of size in ganglion cell receptive fields. They will be much larger in the periphery than in the center, so that they will all have the same number of cones. They will also have the same photon flux per receptor as the ganglion cells in the central portion of the retina under photopic conditions.

The change in size insures that the neural signal generated is proportional to the intensity of the object for the peripheral portion of an object as well as the central portion of it, possibly with regard to adaptation or speed of response, etc.

However, perhaps these are compensatory structural adaptations in order to make the retina work without a lot of complicated neural adjustments. The changes in the shape of the cones and the location of the peripheral retina closer to the lens can both be adaptations of this type.

From all this, it seems that in order to perceive an evenly illuminated scene, many structural adaptations of the retina are required to overcome the unavoidable optical defects in the eye. In the peripheral retina, this increase in the area of the cones and the overall decrease in cone density

both act to require large ganglion cell receptive fields. The data from Wolbarsht and Ringo (1978, 1979, 1980) seems to indicate that each ganglion cell receptive field in the cat retina contains the same number of cones, although a lower retinal density for both cones and ganglion cells will be found toward the periphery. The same may be true of ganglion cells outside of the foveal portion of the monkey retina. This effect produces larger peripheral receptive fields and must be considered when analyzing data concerning them, particularly as related to visual acuity.

Implications Of Changes In Image Size And Retinal Intensity For Peripheral Versus Central Images On The Retina

A balanced view of all aspects of the retinal image and receptor anatomy as discussed in the preceding analyses may be, simply, that the number of receptive fields and the amount of their overlap is the most important factor. Even though the peripheral receptive fields are larger, they are sparse and thus, their centers must be located further apart and have less overlap. All of this means that it is impossible to determine from the present information exactly what limitation on visual acuity is made by the changes in the sizes of receptive fields and their relative density in the periphery.

At the present time, however, the constancy of the number of receptors per receptive field means that the developmental situation is much easier. Probably, this simplifies the analytical problem as regards intensity. From

this, a certain neural signal for a synaptic fiber will mean the same amount of light within any receptive field, whether a large or a small one. Because of this, no highly complex, central processing is necessary to equalize the intensity of the image across the retina on an evenly illuminated object. Also, the background for visual space will appear approximately evenly bright all over the retina because of these anatomical adaptations of the receptors and the ganglion cell receptive fields, rather than any elaborate weighting function in the neural processing. This also could mean that the processing for visual acuity is uniform throughout the retina. From this it can be concluded that in the foveal region of the retina in man, the neural processing that takes place for the highest acuity is similar to that in the rest of the retina. There is not a sharp break in either the anatomical arrangement of the receptive fields or the neural processing of the data arising from them in passing from the fovea to the rest of the retina. Indeed, the high sensitivity to displacement at the border between the center and surround of the ganglion cell receptive field with a saccade may give the strongest neural signal for an edge or disjunction within visual space under physiological conditions. This type of edge detection, then, would impose the ultimate limit to visual acuity. An investigation of the dimensions of the receptive fields in the human fovea could define the proper distance for image displacement, and then by conventional image stabilization techniques, the saccadic movements could be limited to this value. This could insure that the ultimate visual acuity is achieved in any selected operational situation.

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